

New records of molluscs (*Leptoconchus*, *Lithophaga*, *Fungiacava*) that bore Indo-Pacific reef corals and their interactions with their hosts

by Helmut ZIBROWIUS and Patrick M. ARNAUD

Abstract. — New records of the coralliophilid gastropod *Leptoconchus striatus* in *Fungia somervillei* from the Seychelles and of the mytilid bivalve *Lithophaga lima* in *Trachyphyllia geoffroyi* from the Philippines fall within the previously known geographical range. New records of the mytilid bivalve *Fungiacava eilatensis* in *Fungia fragilis*, from Réunion Island and Madagascar, considerably extend the range of this highly cryptic and therefore rarely recorded borer. The fungiid host's conformation appears to influence the shape of the *Fungiacava* individuals. *Fungiacava* may be inaequivalve. Calcareous deposits lining the cavity of the coralliophilid are produced by the coral host, whereas those lining the cavities of both mytilids are produced by the borers. Growing to an excessive size with respect to its coral host in this particular case, *L. lima* had to shift position, its migrating cavity aperture leaving behind a sealed track. This suggests a comparison with the boring behaviour observed in an acrothoracid cirripede (*Lithoglyptes viatrix*) infesting deep-water corals.

Keywords. — Association, chemical borers, *Fungiacava*, *Leptoconchus*, *Lithophaga*, *Fungia*, *Trachyphyllia*, Bivalvia, Gastropoda, Scleractinia, Indo-Pacific.

Résumé. — *Nouvelles signalisations de mollusques (Leptoconchus, Lithophaga, Fungiacava) forant des coraux récifaux de l'Indo-Pacifique et interactions avec leurs hôtes.* Les nouvelles signalisations du gastropode Coralliophilidae *Leptoconchus striatus* chez *Fungia somervillei* des Seychelles et du bivalve Mytilidae *Lithophaga lima* chez *Trachyphyllia geoffroyi* des Philippines s'inscrivent dans l'aire géographique antérieurement connue. Celles du bivalve Mytilidae *Fungiacava eilatensis* chez *Fungia fragilis* de la Réunion et de Madagascar étendent considérablement l'aire connue de ce foreur hautement cryptique et donc rarement signalé. La conformation du Fungiidae disponible comme hôte semble influencer sur la forme des individus de *Fungiacava*. *Fungiacava* peut être inaequivalve. Les dépôts calcaires dans la cavité du Coralliophilidae sont produits par le scleractiniaire hôte tandis que ceux dans les cavités des deux Mytilidae sont produits par les foreurs. Lorsqu'il atteint, dans ce cas particulier, une taille excessive par rapport au scleractiniaire hôte *L. lima* a dû modifier sa position ; la migration de l'ouverture de sa cavité a laissé derrière elle une trace scellée. Cela suggère une comparaison avec le comportement foreur observé chez un cirripède acrothoracique (*Lithoglyptes viatrix*) infestant des coraux de profondeur.

Mots-clés. — Association, foreurs par voie chimique, *Fungiacava*, *Leptoconchus*, *Lithophaga*, *Fungia*, *Trachyphyllia*, Bivalvia, Gastropoda, Scleractinia, Indo-Pacifique.

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INTRODUCTION

Coral-boring gastropod and bivalve molluscs have a long and abundant literature record (surveys in GOREAU *et al.*, 1972; KLEEMANN, 1980, 1990; MORTON, 1990). Points of special interest are the boring mechanism and adaptations to contact with the coral polyp tissues. Here we present new records of three borers (one gastropod, two bivalves) from the tropical Indo-Pacific. These borers are associated with live scleractinian corals. For convenience the coral hosts are here categorized as reef-corals, since all are either from coral reef environments or from just below the level where reefs generally thrive, even though as free soft bottom dwellers they do not contribute to the fabric of the reef.

The mytilid bivalve genus *Lithophaga* Röding, 1798, is known to bore dead and live coral substrates. More restricted, the coralliophilid gastropod genus *Leptoconchus* Rüppell, 1835, is known only from live corals, occupying a wide range of genera and families. The mytilid bivalve genus *Fungiacava* Goreau *et al.*, 1968, occurs only in the free-living Fungiidae.

The degree of concealment of the three borers is also different. The cavities produced by *Lithophaga* are often detectable at the outer surface of the coral substrate. Cavities inhabited by *Leptoconchus* are typically indicated by apertures within the calicular area or, exceptionally, on the lower side of fungoids. Cavities of *Fungiacava* have an aperture deep within the centre of the coral. This may explain why *Fungiacava* is also the least frequently recorded of these three genera and was previously known from few areas. Here, we add records of *Fungiacava* from two new areas in the southwestern Indian Ocean. This is a considerable but not unexpected extension of the geographical range. The new records of the other borers also provide an additional insight into the interaction between the borer and the host.

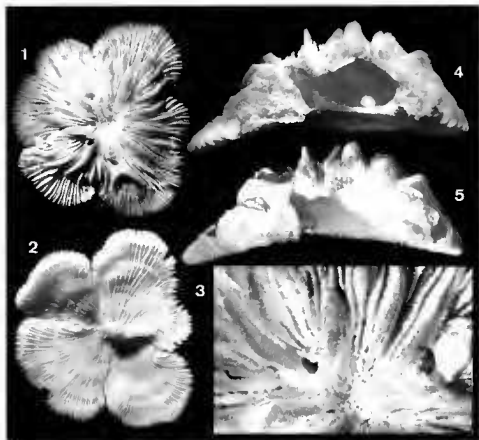
All specimens of boring molluscs reported upon here, together with their coral hosts, are deposited in the mollusc collection of the Muséum national d'Histoire naturelle, Paris (MNHN).

1. *Leptoconchus striatus* in *Fungia somervillei*

(Figs 1-5)

All species of *Leptoconchus* Rüppell, 1835 [= *Magilopsis* Sowerby, 1919] (Coralliophilidae) bore in live Indo-Pacific reef corals of various genera and families (MASSIN, 1982). They are characterized by a high intraspecific morphological variability and sexual dimorphism. We agree with BOULLON *et al.* (1981) and MASSIN (1982, 1989) that *Leptoconchus* is distinct from *Magilus* Montfort, 1810, with which it had occasionally been synonymized.

Some *Leptoconchus* from the Egyptian Red Sea have been studied in detail by GOHAR & SOLIMAN (1963). A series of papers by BOULLON *et al.* (1981) and MASSIN (1983, 1989, 1990) focused on northern Papua-New Guinea and provided detailed information on various species, including on host specificity. HOEKSEMA (1993, fig. 7) illustrated a *Leptoconchus* infested fungiid from that area. Another new record is from Komodo Island, Indonesia (HOEKSEMA & ACHITUV, 1993).



Figs 1-5. — *Fungia somervillei* bored by *Leptoconchus striatus*, Seychelles (width of coral 28 mm). 1, upper side with pair of apertures near centre; 2, lower side; 3, central area of upper side with apertures; 4 and 5, views into the cavities of the transversely broken coral, in 4 light falling in through aperture of larger cavity.

NEW RECORD FROM THE SEYCHELLES

Fisheries investigations carried out on the Seychelles Plateau by the ORSTOM vessel "Coriolis" in 1980 (cruise REVES 2) produced a few fungiid corals (3 hauls, 44-54 m): *Fungia* (*Cycloseris*) sp., *F. (Cycloseris) somervillei* Gardiner, 1909, and *F. (Wellsofungia) granulosa* Klunzinger, 1879; all identified by B.W. HOEKSEMA (MNHN).

Fungia somervillei (figs 1-5) is represented by one specimen (stat. 55, dredge, 17.9.1980, 3°48'S, 55°06'E, 54 m, SW Bird Island). For a detailed account of this species see HOEKSEMA (1989). The maximum diameter of the regenerated irregular coral (figs 1-2) is 28 mm, the height 10.5 mm. The upper central part is strongly convex, as is typical of this species. The specimen consists of 4 unequal and irregular main lobes. Its concave lower side is marked by radial slits

between the lobes that extend towards the centre (fig. 2), facilitating fragmentation into wedge-shaped pieces.

Collected alive, this coral contained two specimens of *Leptoconchus striatus* Rüppell, 1835, concealed in their cavities. Unfortunately this was noticed only after the polyp tissues had been partially removed with hypochlorite and the coral dried. Given this treatment, little more than shells were left, but enough to identify them beyond doubt as *L. striatus*, and to record, in the larger, female specimen, the ovigerous sacs containing larvae, as already described by DESHAYES (1863) and BOUILLON *et al.* (1981). The male shell measures 2.7 mm in height and 1.9 mm in width, the female shell 3.8 mm in height and 6.1 mm in width. Their shape is similar, respectively, to that in figures 4 d and 4 f-g of BOUILLON *et al.* (1981).

L. striatus was already known from the Red Sea (type locality), Seychelles, Réunion, Mauritius, Papua-New Guinea, New Caledonia and Japan. Our new record falls within this range.

CAVITIES PRODUCED BY *L. striatus*

Two small, upwardly directed, apertures in the high central part of the coral (figs 1, 3), about 5 mm distant from each other, mark the entrances to the cavities, each contained in a different main lobe of the coral. A smaller, subcircular, aperture (0.8 × 1.0 mm) opens into the smaller cavity of the male (3.5 mm high and less wide), a larger, elongate, aperture (1.2 × 1.6 mm) into the larger cavity of the female (6.5 mm wide and less high). Both cavities communicate (figs 4-5), permitting contact between their inhabitants. For similar observations of sexual dimorphism see MASSIN (1989).

In the central upper part of the coral and especially near the apertures, there is evidence that the coral polyp reacted against the boring activity by adding sclerenchyme between the septa. Inside the cavities, the septa look like "sectioned". Neither the cavities nor the apertures have a calcareous lining secreted by the gastropod.

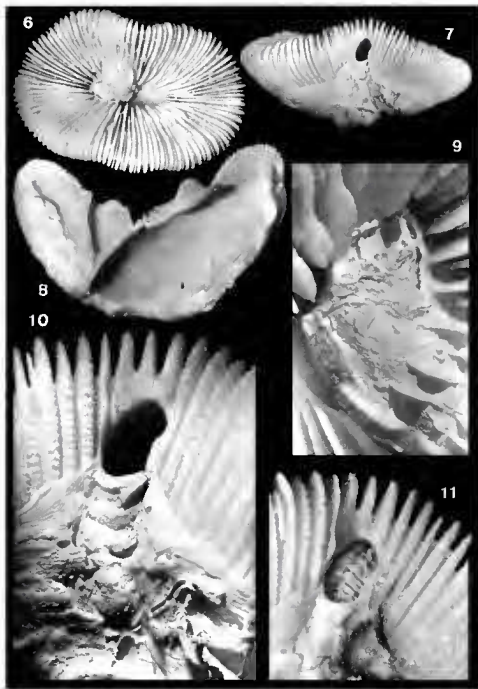
2. *Lithophaga lima* in *Trachyphyllia geoffroyi*

(Figs 6-11)

The genus *Lithophaga* Röding, 1798, with some 25 species in tropical and temperate waters (KLEEMANN, 1983), has been recorded in a wide range of substrates, including colonial and solitary scleractinian corals, dead and alive. It is now widely accepted that *Lithophaga* bores chemically, not mechanically. According to KLEEMANN (1990: 113) any mechanical boring process should be regarded as secondarily developed, requiring more adaptive evolutionary steps than chemical boring.

NEW RECORD FROM THE PHILIPPINES

Two specimens of *Lithophaga (Leiosolenus) lima* Jousseume MS in LAMY, 1919, are recorded in one *Trachyphyllia geoffroyi* (Audouin, 1826) from the Philippines ("Coriolis", cruise MUSORSTOM 3, stat. 142, 6.6.1985, 11°47'N, 123°01.5'E, 26-27 m).



FIGS 6-11. — *Trachyphyllia geoffroyi* bored by *Lithophaga lima*, Philippines (larger diameter of coral 62 mm). 6, calice with repair of ruptured cavity in columella area; 7, side view with aperture; 8, transverse section showing cavity with calcareous lining in the upper part; 9, bulging repair of ruptured cavity in columella area; 10, upwards migrated aperture with calcareous sealing beneath marked by distinct growth steps; 11, posterior end of bivalve with calcareous ridges visible inside aperture, with smooth siphon area above (also in 10).

The coral host fits information on *Trachyphyllia geoffroyi* in VERON *et al.* (1977). Typical of soft bottoms in reef environments, *T. geoffroyi* occurs from the Red Sea through the Philippines to southern Japan, New Caledonia and eastern Australia. Young stages start attached to a small substrate and pass through a regular flabelloid stage before becoming meandroid (intramural budding in short series). Transition is marked by a lateral constriction, the depression being perpendicular to the calicular edge on the concave side.

The bored coral (figs 6-11) conforms the flabelloid stage, with a slight constriction (vertical depression) on one side (fig. 6); height 30 mm, calice 34-38 × 62 mm. It was dead when collected and bears a few tiny spirorbid tubes attached to septa within the calice. The two bivalves had survived their host. This and the excellently preserved calicular structures indicate that the death of the coral was most recent and subsequent to the deep transverse boring by *L. lima*.

The type material of *Lithophaga lima* was from "Djibouti, Aden" and LAMY (1919, 1937) considered *L. nasuta sensu* Dunker, 1882, from the Philippines, as conspecific. According to LAMY, the true *L. nasuta* (Philippi, 1846) was known from "Mozambique, Zanzibar, Manila, Japan, etc.". Wilson (1979) redescribed *L. lima* and recorded it from the Indo-West Pacific: Japan, Philippines, Malaysia, Indonesia, Papua-New Guinea (Bismarck Archipelago), Solomon Islands and northern Australia). But misunderstanding LAMY, he also erroneously included LAMY's records of the true *L. nasuta* under *L. lima*. SCOTT (1980) found *L. lima* from live corals at Hong Kong. Including KLEEMANN's (1980) records the known distribution of *L. lima* is: Red Sea, Kenya, Mozambique, Seychelles, Chagos, Maldives, Malaysia, Indonesia, Papua-New Guinea, Solomon Islands, northern Australia, Philippines, Hong Kong, Japan. Our new record falls within this range.

The larger bivalve from *T. geoffroyi* fits both the original and WILSON's (1979) descriptions of *L. lima* by its shape and calcareous coating of the shell. The raised calcareous ridges of the coating are "radial and divaricate near the posterior margin", and end close to the posterior margin of the valves in a "serrated edge", as indicated by WILSON (1979). On the outer side of the shell a radial purple ray (LAMY's "rayon violet") occurs only on the left valve, whereas on the inner side a purple tinge is present on both valves, but does not sharply form a ray. The shell length is only 25.0 mm, whereas WILSON (1979) indicates 80.5 mm for the largest syntype. The smaller specimen obtained is only 7.3 mm long and is supposed to be a juvenile of *L. lima*.

Inside their cavities, the bivalves were oriented dorsal side down, a feature already recorded for other coral-boring mytilids: *Fungiacava ellatensis* (cf. GOREAU *et al.*, 1969; present paper), *Lithophaga lessepsiana* (cf. ARNAUD & THOMASSIN, 1976) and *Botula cordata* (cf. SAVAZZI, 1982).

CAVITIES PRODUCED BY *L. lima*

The cavity of the larger bivalve extends from one side of the coral to the other. The aperture is in the median line of the constricted (concave) area of the coral (fig. 7). It is elongate and nearly upright in position, 5.7 mm high and 3.3 mm wide, and about 5 mm below the upper edges of the nearest septa (figs 10-11). The cavity is directed obliquely downwards to the opposite, convex, side of the lower part of the coral, where the skeleton is particularly massive. Here, by enlarging anteriorly the cavity, the bivalve ruptured the coral wall, creating a small

“accidental” aperture. Inside the coral when split in two along the cavity (fig. 8), the wall near the functional aperture is lined by a calcareous deposit produced by the bivalve. Elsewhere, “sectioned” septa can be seen in the bare wall. Growth of the larger bivalve and of the coral influenced each other. Conspicuous modifications concern the position of the aperture and the orientation of the cavity (see below).

The cavity of the smaller bivalve, normal in having only one aperture, is situated below the cavity of the larger bivalve on the convex side of the coral. Confined to the massive lower part and distant from the polyp tissues, the smaller bivalve did not interfere otherwise with the coral.

INTERACTION OF CORAL AND BIVALVE

The aperture of the larger bivalve close to the calicular edge represents its present functional stage. It had been moving upwards from a previous position at least 10 mm below the present one. Jointly, it had undergone an elongation, matching the progression of the growing coral's calicular edge. This elongation of the aperture was compensated for by progressive obstruction of its former lower part by means of a calcareous deposit produced by the bivalve and marked by distinct (annual?) growth steps (fig. 10).

Upward-moving of the aperture is explained as follows. After the bivalve larva had settled on the coral and penetrated perpendicularly to the surface, it was not limited by boreable substrate thickness. When it grew longer and thicker in its steadily enlarging cavity, it became limited, at the initially bored level, by the non-increasing width of the coral. Accordingly, the bivalve could no longer both be contained and continue to grow in this position. The accidental aperture (facing the anterior end of the shell) illustrates this limitation. The bivalve had to shift into an oblique position compatible with further growth and cavity enlargement. A similar reorientation capability was observed by KLEEMANN (1974) in the Mediterranean *Lithophaga lithophaga* and by SCOTT (1988) in the Caribbean *Lithophaga bisulcata*.

Reorientation of the bivalve caused the cavity to open into the axial fossa of the coral. This “accidental” rupture was closed by means of a calcareous deposit produced by the bivalve (figs 6, 9). The larger the penetration into the fossa, the more replacement of coral structures was needed to seal the cavity. The resulting bulging repair covers about half of the columella area and extends between adjacent paliform lobes and septa (figs 8-9). It is situated a few millimeters above the level of the remaining half of the columella. Below that repair, all the previous coral structures have disappeared (columella, paliform lobes and septa). The new wall is an irregular patchwork (fig. 9) resulting from distinct smaller ruptures and repairs. A similar sealing is observed where *Fungiacava* extends its cavity in small fungiids (this paper).

On the constricted side of the coral, on top of the aperture, the calicular edge protrudes higher than elsewhere (fig. 7). Locally increased growth seems related to the bivalve's siphons protruding from the aperture and being directed upwards. Modified growth may be either an avoidance reaction towards the bivalve or be induced by the waterflow canalized by the siphons.

Lower in the constriction, the extension of the distinct, thin, epitheca produced by the retreating edgezone of the coral polyp, is also modified. Elsewhere, the epitheca covers approximately the lower half of the coral (fig. 7), its upper limit indicating the range of the

edgezone. In the constriction, the epitheca extends to a much higher level, up to both sides of the aperture (fig. 10). This is explained by the aperture being an obstacle to the edgezone. Accordingly, the sealed area below the present functional aperture (fig. 10) is out of reach of the edgezone and, therefore, is not covered by epitheca.

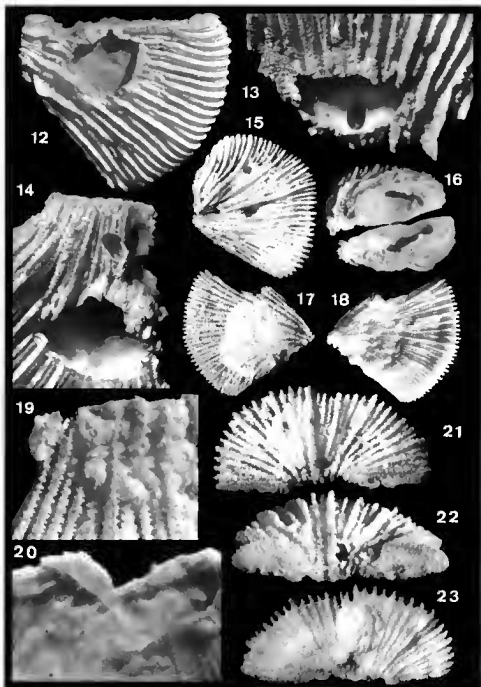
One more modification of the coral can be seen in the constriction between the aperture and the calicular edge. Here a smooth, narrow, depression runs along the three costae just above the aperture (figs 10-11). The median costa is smooth throughout its width, whereas the others are smooth in the part adjacent to the median costa. They are, thus, unlike all other costae that, at the same level, are prominent and bear a characteristic sculpture of regularly arranged granules. The narrow, bare and smooth surface looks much like the inner surface of the cavity where the latter is not covered by the calcareous lining produced by the bivalve: the costae look like "sectioned", their outer parts "cut" away. A similar aspect suggests a similar cause: all such surfaces have been in contact with the tissues of the bivalve, those inside the cavity with the mantle, those in the outer depression with the upwardly directed siphons. This is fully consistent with the generally accepted hypothesis of chemical boring in *Lithophaga* and other mytilids.

3. *Fungiacava eilatensis* in *Fungia fragilis*

(Figs 12-23)

Fungiacava eilatensis GOREAU *et al.*, 1968, is a delicately shelled small bivalve (Mytilidae, Lithophaginae) living in a cavity inside the free-living stages of fungiid corals. The discovery of this form at Eilat, Red Sea, prompted several publications by GOREAU *et al.* (1968, 1969, 1970, 1972, 1976). The literature comprises only few additional records (BOUILLON *et al.*, 1981; KLEEMANN, 1992; HOEKSEMA & ACHITUV, 1993). Distribution and the host corals have been listed by HOEKSEMA & ACHITUV (1993), who also revised part of the earlier host identifications [below between brackets], following HOEKSEMA's (1989) monograph of the Fungiidae. Surprisingly, HOEKSEMA (1989) had not mentioned *Fungiacava*.

Previous observations on host size, depth and infestation rates are summarized here. The potentially large-growing *Fungia* (*Lobactis*) *scutaria* (Lamarck, 1801) [as "*Pleuactis*"] and *Fungia* (*Fungia*) *fungites* (Linnaeus, 1758) are the hosts at Eilat on the shallow reef and further south along the Sinai coast. Depending on locality, 8-80 % of a population of *F. scutaria* are infested by *F. eilatensis* (one to several bivalves per coral). GOREAU *et al.* (1969) examined thousands of fungiids from other areas but only a collection from the Maldives provided, for one station, a notable infestation rate: 16 % of the small *Fungia* (*Cycloseris*) *sinensis* Milne Edwards & Haime, 1849 [as "*Diaseris distorta*"] from 50-80 m, contained the bivalve. Occasional hosts in the Maldives were *Fungia* (*Cycloseris*) sp. [as "*Diaseris*"] and *Fungia* (*Cycloseris*) *fragilis* (Alcock, 1893) [as "*Diaseris sinensis*"], both from 50 m, and *Fungia* (*L.*) *scutaria* and *F. (F.) fungites*, both from shallow water. Elsewhere, only two individuals were found infested: *Fungia* (*Cycloseris*) *fragilis* (Alcock, 1893) [as "*Diaseris*"] from "East Indian Archipelago or Australia" and *Fungia* (*L.*) *scutaria* from the Marshall Islands. GOREAU *et al.* (1969) concluded that *Fungiacava eilatensis* has a sporadic and disjunct distribution, compared with that of its hosts. An occasional observation of *F. eilatensis* is from Safaga, Red Sea coast of Egypt, in *Fungia fungites* (KLEEMANN, 1992). In northern Papua-New Guinea, it was found



FIGS 12-23. — *Fungia fragilis* bored by *Fungiacava eilatensis*, Madagascar (12-14), Réunion (15-23). 12, specimen (width 19 mm) with cavity broken open; 13, 14, same, aperture from inside and outside the cavity. 15, specimen (width 13 mm) with almost complete cavity wall from above; 16, same, split, showing cavity; 17, upper side of specimen (width 11.7 mm) with complete cavity wall; 18, same, lower side with small bulging repairs; 19, 20, same, upper cavity wall from outside and inside; 21, smallest bored specimen (width 8.7 mm); 22, upper side, oblique view with repair; 23, lower side with large bulging repair.

in a single *Fungia* sp. (BOUILLON *et al.*, 1981), and in two *Fungia* (*Cycloseris*) *tenuis* Dana, 1846 (HOEKSEMA & ACHITUV, 1993), out of hundreds of fungiids from the reefs. In that area, with a well studied and highly diverse fungiid fauna (HOEKSEMA, 1993), the infestation rate is low. Likewise, at Komodo Island, Indonesia, HOEKSEMA & ACHITUV (1993) obtained only three specimens from *Fungia* (*C.*) *fragilis*.

NEW RECORDS FROM THE SW INDIAN OCEAN

Our records of *Fungiacava eilatensis* from the SW Indian Ocean are the first from that area. The coral host is *Fungia* (*Cycloseris*) *fragilis* (Alcock, 1893), one of the species previously recorded from other areas as a host of the bivalve (see above). For a detailed account of *F. fragilis*, see HOEKSEMA (1989). This widely distributed Indo-Pacific species occurs commonly as irregular regenerating wedge-shaped fragments but regeneration may result in secondarily subcircular specimens.

From Réunion Island (Mascarene Islands): The 1982 "Marion Dufresne" cruise MD 32 obtained mostly dead and often eroded fungiids from 11 hauls (50 m and deeper on the steep insular slope). The collection (MNHN), for the greater part identified by B.W. HOEKSEMA, comprises five species, with up to three occasionally co-occurring per station: *Fungia* (*Cycloseris*) *cyclolites* Lamarck, 1816; *F. (C.) distorta* Michelin, 1842; *F. (C.) fragilis* (Alcock, 1893); *F. (C.) sinensis* Milne Edwards & Haime, 1849; *F. (C.) vaughani* Boschma, 1923. Five additional dead and damaged small *Fungia fragilis* (identified by H.Z.) were infested by *Fungiacava* (three illustrated herein, figs 15-23); all are from one station (stat. DC 176, 8.9.1982, 21°01.7'S, 55°10.6'E, 165-195 m, off Cape Houssaye). All infested corals contained fragmentary or complete shells of the bivalve.

From Madagascar: During a cruise for the ORSTOM laboratory of Nosy Bé, in 1970, various biological samples were obtained by R. PLANTE from Pracel Bank, a large shelf extension along northwestern Madagascar. Several dead and damaged small fungiids were obtained, including two *Fungia fragilis* (identified by H.Z.) with *Fungiacava* cavities (stat. BP 10, 9.4.1970, 16°22.5'S, 43°39.5'E, 50 m). The cavity in the larger eroded coral (figs 12-14) was open and no longer contained the bivalve. The cavity in the smaller coral contained poorly preserved shell fragments.

All corals with *Fungiacava* cavities are regenerated. The smallest of the Réunion specimens (figs 21-23), nearly half-circular, has a radius of 4.6 mm and a width of 8.7 mm; the largest is irregularly wedge-shaped and has a radius of 12.3 mm and a width of 15 mm. Both corals from Madagascar are wedge-shaped, the smaller one with a radius of 9 mm and a width of 17.7 mm; the larger one (fig. 12) with a radius of 19 mm and a width of 19.5 mm. The narrow end with the centre of septal divergence generally resembles what can be found in the centre of regular circular specimens. By analogy, this zone is hereafter called the "centre".

CAVITIES PRODUCED BY *F. eilatensis*

The cavity always occupies an area near the "centre" of the irregular regenerating corals and in the smaller ones may even extend to near the periphery whereas in the larger specimens it covers about half the radius. The width of the cavity is about equal to its length. The largest

cavity (in the larger Madagascar coral) is 7.5 mm long and 7 mm wide, but only 2 mm high (fig. 12). The cavity spreads through many septa (up to 50 or 60 when counted peripherally). Typically, it is sealed all round, except for an outlet towards the "centre". This aperture corresponding to the siphon may be a short and slightly compressed tubular structure, 1-2 mm long (figs 13-14). In the larger coral from Madagascar, with also the largest cavity (see above), the outlet measures 0.9×1.4 mm in cross section. The cavity wall and the short aperture tube are part of a smooth calcareous coating produced by the bivalve. Given the small size of the irregular regenerating host corals and, in particular, their reduced height, the cavities tend to extend through all the height and occasionally to attain the lower face (figs 18, 22). The coating of the cavity thus becomes evident from above (figs 12-15, 17) and occasionally also from below (figs 21, 23). Externally this secondary wall is composed of adjacent small bulging domes (figs 19-20). It is a patchwork of nonsynchronous small-surface dissolution and secretion areas, resulting from a dynamic compromise between growth of the bivalve and confinement, respectively.

In the cavities the shells lie on their flat dorsal side (conforming to the flat bottom of the host coral), the posterior end directed towards the tubular aperture near the "centre", the umbones directed towards the periphery (position already observed by GOREAU *et al.*, 1969).

SIZE AND SHAPE OF *Fungiacava* SHELLS

By their depressed heart-shape, the sculpture of fine concentric riblets and by being extremely thin and fragile, the shells from Réunion Island correspond to previous descriptions and illustrations.

Individual proportions show some variation. The largest shell is also the best preserved, comprising two fairly complete valves (length 5.6 mm, width 5.8 mm, height 1.8 mm). It is slightly wider than long, a proportion that also characterizes the specimen illustrated by HOEKSEMA & ACHITUV (1993, fig. 1). The Réunion specimens are smaller than those reported previously (GOREAU *et al.*, 1969: up to 14 mm; BOUILLON *et al.*, 1980: 7.4 mm; HOEKSEMA & ACHITUV, 1993: about 10 mm, here extrapolated from their figures 1-2).

Shell asymmetry in *Fungiacava* has not yet been mentioned. However, some specimens proved to be inaequivalve. The left valve of the largest Réunion shell is about 7 % wider than the right; conversely, in a smaller shell the right valve is about 6 % larger than the left; the valves of the other shells are either subequal or too much damaged for precise comparison. In case shells illustrated in the literature are shown in a strictly vertical position, they also appear to be inaequivalve (GOREAU *et al.*, 1969, pl. 1 a-b; HOEKSEMA & ACHITUV, 1993, fig. 1).

It had been noted that specimens of *Fungiacava* from "deeper water" in the Maldives are somewhat different from those from the shallow type locality at Eilat. They were said to be "consistently smaller, flatter and rather broader in proportion to the length than their shallow water relatives". The deeper water form was for convenience named *Fungiacava eilatensis* "forma *gardineri*" (GOREAU *et al.*, 1969: 176, 179). The secondary literature, when mentioning this form, does not provide complementary data (KLEEMANN, 1980, 1990; BOUILLON *et al.*, 1981; MORTON, 1983, 1990).

The shells extracted from the small wedge-shaped *Fungia fragilis* from Réunion Island also appear flatter and broader than the type series of *F. eilatensis* from the larger *Fungia scutaria*

from Eilat and thereby resemble the "forma *gardineri*". The corals from Réunion Island (and Madagascar) may be the smallest ones that have been recorded as hosts for *Fungiacava*, unless those with "forma *gardineri*" from the Maldives were of similar small size.

"Forma *gardineri*" could be a matter of the smaller size and height of the hosts, shape and size of *F. eilatensis* depending simply on the shape and size of the fungiid host with which the bivalve has to cope.

GENERAL REMARKS AND CONCLUSIONS

There is no evidence that the three borers studied here bore other than by chemical means only. In the wall of cavities, the septa look like "sectioned", similar to what has been observed (SAVAZZI, 1982) in an Eocene coral bored by the mytilid *Botula cordata* and in cavities produced in Recent corals by crustaceans, e. g., Ascothoracida (ZIBROWIUS & GRYGIER, 1985) and Decapoda Cryptochiridae (ZIBROWIUS & GILL, 1990).

The coralliophilid gastropod *Leptoconchus striatus* causes the coral polyp to produce additional sclerenchyme as an interseptal filling, an unsuccessful attempt to seal off the borer. But this does not cause a conspicuous gall of the type commonly formed around invading ascothoracids (buildups of spongy sclerenchyme). In the presence of the mytilid bivalves *Lithophaga lima* and *Fungiacava eilatensis*, the coral polyp does not react by producing a calcareous wall around the intruder, but a calcareous deposit lining the cavity is secreted by the mollusc: *F. eilatensis* produces a wall and a small calcareous siphonal outlet; *L. lima* also produces a wall and, in the special case studied here, seals part of its elongate aperture. Like other boring mytilids, *F. eilatensis* and *L. lima* illustrate a common paradox. They dissolve calcium carbonate to enlarge the cavity and they secrete it to line the cavity and to seal ruptures (see also SCOTT, 1988).

The case of *Lithophaga lima* boring the reef coral *Trachyphyllia geoffroyi* suggests a comparison with that of the acrothoracican cirriped *Lithoglyptes viatrix* boring branches of the deep-water scleractinian *Enallopsammia* (see GRYGIER & NEWMAN, 1985). *L. viatrix* bores long horizontal cavities across the coral surface, possibly in an attempt to move to or to maintain a more favourable position. Subsequently, the resulting apertural slit is superficially sealed by a calcareous cement deposit and the cirriped's ever-growing calcareous rostrum. This results in a functional terminal aperture followed by an elongate trail contrasting with the surrounding coral surface. Motility of the aperture and sealing off its older parts are a striking convergence in two widely distinct zoological groups.

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REFERENCES

- ARNAUD, P. M., & B. THOMASSIN, 1976. — First records and adaptive significance of boring into a free-living scleractinian coral (*Heteropsammia michelini*) by a date mussel (*Lithophaga lessepsiana*). *Veliger*, **18**: 367-374.
- BOUILLON, J., C. MASSIN & J. VAN GOETHEM, 1981. — *Fungiacava eilatensis* Soot-Ryen, 1969 (Bivalvia, Mytilidae) et *Leptoconchus striatus* Rüppell, 1835, (Gastropoda, Coralliophilidae), mollusques perforant des *Fungia* (Anthozoa, Fungiidae) récoltés en Papouasie-Nouvelle-Guinée. *Acad. Sci. Outre Mer, Bull. Séanc.*, Cl. Sci. nat. med., Bruxelles, **1980** (4): 549-570.
- DESHAYES, G. P., 1863. — Catalogue des mollusques de l'île de la Réunion. In: *Notes sur l'île de la Réunion*, L. MAILLARD. Paris, Dentu: 144 p., 14 pl.
- GOHAR, H. A. F., & G. N. SOLIMAN, 1963. — On the biology of three coralliophilids in living coral. *Publ. mar. biol. Stat. Ghardaqa*, **12**: 99-126, pl. 1.
- GOREAU, T. F., N. I. GOREAU, Y. NEUMANN, & C. M. YONGE, 1968. — *Fungiacava eilatensis* n. gen., n. sp. (Bivalvia, Mytilidae), a boring bivalve commensal in reef corals. *Amer. Zool.*, **8**: 799.
- GOREAU, T. F., N. I. GOREAU, T. SOOT-RYEN, & C. M. YONGE, 1969. — On a new commensal mytilid (Mollusca: Bivalvia) opening into the coelenteron of *Fungia scutaria* (Coelenterata). *J. zool. Soc.*, **158**: 171-195.
- GOREAU, T. F., N. I. GOREAU, C. M. YONGE, & Y. NEUMANN, 1970. — On feeding and nutrition in *Fungiacava eilatensis* (Bivalvia: Mytilidae), commensal living in fungiid corals. *J. zool. Soc.*, **160**: 159-1720.
- GOREAU, T. F., N. I. GOREAU, & C. M. YONGE, 1972. — On the mode of boring in *Fungiacava eilatensis* (Bivalvia: Mytilidae). *J. zool. Soc.*, **166**: 55-60.
- GOREAU, T. F., N. I. GOREAU, & T. J. GOREAU, 1976. — *Fungiacava eilatensis* burrows in fossil *Fungia* (Pleistocene) from the Sinai Peninsula. *Proc. roy. Soc. London*, **193**: 245-252, pl. 36-39.
- GRYGIER, M. J., & W. A. NEWMAN, 1985. — Motility and calcareous parts in extant and fossil Acrothoracica (Crustacea: Cirripedia), based primarily upon new species burrowing in the deep-sea scleractinian coral *Enallopsammia*. *Trans. San Diego Soc. nat. Hist.*, **21**: 1-22.
- HOEKSEMA, B. W., 1989. — Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). *Zool. Verhand.*, **254**: 295 p.
- HOEKSEMA, B. W., 1993. — Mushroom corals (Scleractinia: Fungiidae) of Madang Lagoon, northern Papua New Guinea: an annotated check-list with the description of *Cantharellus jebbi* spec. nov. *Zool. Meded.*, **67**: 1-18.
- HOEKSEMA, B. W., & Y. ACHITUV, 1993. — First Indonesian record of *Fungiacava eilatensis* Goreau et al., 1968 (Bivalvia: Mytilidae), endosymbiotic of *Fungia* spp. (Scleractinia: Fungiidae). *Bacteria*, **57**: 131-138.
- KLEEMANN, K., 1974. — Raumkonkurrenz bei Ätzmuscheln. *Mar. Biol.*, **26**: 361-364.
- 1980. — Boring bivalves and their host corals from the Great Barrier Reef. *J. moll. Stud.*, **46**: 13-54.
- 1983. — Catalogue of recent and fossil *Lithophaga* (Bivalvia). *J. moll. Stud.*, Suppl. **12**: 1-46.
- 1990. — Evolution of chemically-boring Mytilidae (Bivalvia). In: *The Bivalvia* (B. MORTON, ed.) - Proceedings of a memorial symposium in honour of Sir Charles Maurice YONGE (1899-1986), at the 9th International Malacological Congress (1986, Edinburgh, Scotland, U. K.), Hong Kong Univ. Press: 111-124.
- 1992. — Coral communities and coral-bivalve associations in the northern Red Sea at Safaga, Egypt. *Facies*, **26**: 1-10.

- LAMY, E., 1919. — Les lithodomes de la mer Rouge (d'après les matériaux recueillis par M. le Dr JOUSSEAUME). *Bull. Mus. nat. Hist. nat.*, **25**: 252-256, 344-350.
- 1937. — Révision des Mytilidae vivants du Muséum national d'Histoire naturelle de Paris. *J. Conchyl.*, **81**: 99-132, 169-185.
- MASSIN, C., 1982. — Contribution to the knowledge of two boring gastropods with an annotated list of the genera *Magilus* Montfort, 1810, and *Leptoconchus* Rüppell, 1835. *Bull. Inst. roy. Sci. nat. Belg.*, **53** (17): 1-28.
- 1983. — Note on the genus *Leptoconchus* Rüppell, 1835 (Mollusca, Gastropoda, Coralliophilidae) with the description of two new species, *Leptoconchus vangoethemi* sp. n. and *Leptoconchus cyphastreae* sp. n. *Bull. Inst. roy. Sci. nat. Belg.*, (Ser. Biol.) **55** (1): 1-16, pl. 1-5.
- 1989. — Boring Coralliophilidae (Mollusca, Gastropoda): coral host relationship. *Proc. 6th Intern. Coral Reef Symp.*, Townsville 1988, 3: 177-184.
- 1990. — Biologie et écologie de *Leptoconchus peronii* (Lamarck, 1818) (Mollusca, Gastropoda, Coralliophilidae) récolté en Papouasie-Nouvelle Guinée avec une redescription de l'espèce. *Bull. Inst. roy. Sci. nat. Belg.*, (Ser. Biol.) **60**: 23-33.
- MORTON, B., 1983. — Coral associated bivalves of the Indo-Pacific. In: *The Mollusca*, (W.D. RUSSELL-HUNTER, ed.) Volume 6, Ecology. Academic Press: 139-224.
- 1990. — Corals and their bivalve borers. The evolution of a symbiosis. In: *The Bivalvia* (B. MORTON, ed.) — Proceedings of a memorial symposium in honour of Sir Charles Maurice YONGE (1899-1986), at the 9th International Malacological Congress (1986, Edinburgh, Scotland, U. K.), Hong Kong Univ. Press: 11-46.
- SAVAZZI, E., 1982. — Commensalism between a boring mytilid bivalve and a soft bottom coral in the Upper Eocene of northern Italy. *Paläont. Z.*, **56**: 165-175.
- SCOTT, P. J. B., 1980. — Associations between scleractinians and coral-boring molluscs in Hong Kong. In: *The malacofauna of Hong Kong and Southern China (Hong Kong)* (B. MORTON, ed.). Hong Kong Univ. Press: 121-138.
- 1988. — Distribution, habitat and morphology of the Caribbean coral and rock-boring bivalve *Lithophaga bisulcata* (d'Orbigny) (Mytilidae: Lithophaginae). *J. moll. Stud.*, **54** (1): 83-95.
- VERON, J. E. N., M. PICHON, & M. WISMAN-BEST, 1977. — Scleractinia of Eastern Australia, Part II: Familles Faviidae, Trachyphylliidae. *Austr. Inst. mar. Sci. Monogr. Ser.*, **3**: 233 p.
- WILSON, B. R., 1979. — A revision of Queensland lithophaginine mussels (Bivalvia, Mytilidae, Lithophaginae). *Rec. Austr. Mus.*, **32**: 435-489.
- ZIBROWIUS, H., & J. M. GILL, 1990. — Deep-water Scleractinia (Cnidaria: Anthozoa) from Namibia, South Africa, and Walvis Ridge, southeastern Atlantic. *Scientia mar.*, **54**: 19-46.
- ZIBROWIUS, H., & M. J. GRYGIER, 1985. — Diversity and range of scleractinian coral hosts of Ascothoracida (Crustacea: Maxillopoda). *Ann. Inst. océanogr.*, Paris, **61**: 115-138.